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THE STUDY OF POPULATIONS OF LEPIDOPTERA BY CAPTURE-RECAPTURE METHODS

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INTRODUCTION

RECENTLY KILDUFF (1973) presented mark-release-recapture data on a population of the butterfly *Euptychia hermes* from which he determined daily population size and a maximum life expectancy. Fosdick (1973) has used identical methods in his study of the butterfly *Anartia amalthea.* Unfortunately those employed for analysing the population size are inefficient when such extensive multiple recapture data are available, and in addition they violate the assumptions implicit in the underlying mathematical model. Furthermore, the method used for estimating the maximum life expectancy is spurious, since it ignores variation in the number of adults released and the ease with which butterflies were captured from day to day.

Since many people are now using mark-release-recapture methods for studying populations we think it appropriate to mention some of the best available modern methods in order that people can analyse their data efficiently. For the purpose of this paper it would have been convenient to analyse the data of Kilduff and Fosdick but, unfortunately, they are given in such a way that they cannot be analysed by modern methods. Thus, Kilduff tells us that the numbers in the body of his trellis diagram refer to individuals recaptured. However, where a butterfly has been recaptured more than once it is not clear whether the entry in the diamond is appropriate for the first time the insect was captured or the last time, or if recaptured more than twice for some intermediate time. Fosdick declares that in his diagram the numbers also refer to individuals. Nevertheless from Table 1 in his paper it can be seen that the total (189) is greater than the total number of individuals (92). Consequently it seems appropriate not only to suggest efficient methods of analysis but also how the data should be presented in order that the reader may analyse it by modern methods should the author not care to do so.

CAPTURE-RECAPTURE METHODS

Many populations of mobile animals can be investigated using capture-recapture methods. The intuitively easy to understand Lincoln Index (or Petersen estimator) is the simplest and is the basis of more complex mathematical models

$$P = \frac{M_1 N_2}{R_2}$$

where

- P is the population estimate on days 1 and/or 2 (see below)
- M_1 is the number marked and released into the population on day 1
- N_2 is the number captured on day 2
- R_2 is the number of recaptures on day 2

When R_2 is large (i.e. over about 20) the estimate of P is fairly unbiased but if there are fewer recaptures Bailey (1951, 1952) has shown that the estimate tends to be too large and is less biased if 1 is added to N_2 and R_2.

$$P = \frac{M_1(N_2+1)}{(R_2+1)}$$

This correction can also be used in the modified Lincoln Index incorporated in multiple recapture models.

The Lincoln Index makes certain assumptions:

1) Marking does not affect animals and marks are not lost.
2) The marked animals mix randomly in the population.
3) The population is sampled at random. An animal's age, sex or mark does not influence its chance of being captured (see later).
4) Either there is no birth or immigration (dilution) or there is no death or emigration (loss). If there is no dilution but loss the estimate is valid for the population on the day of release. On the other hand if there is dilution but no death then the estimate is valid for the day of recapture.
5) Sampling must be performed at discrete time intervals and the time spent sampling must be negligible (in real terms this means that it must be small) in relation to the inter-sampling period.

Most of the multiple capture-recapture models derived from the Lincoln Index try to remove assumption 4 to make allowance for dilution and loss and they more obviously attempt to represent a *real* animal population. The most popular approaches are listed in Table 1. In general, as one proceeds down this table, one is dealing with methods that need increasing amounts of data (in the form of recaptures). However the models are increasingly realistic and give a more complete series of estimates of parameters of the population. In a capture-recapture study, the type of analysis will depend on the amount of data that can be obtained. Thus where comparatively few recaptures are made Fisher and Ford's method may be the most appropriate, but where more data are available Jolly's, or even Manly & Parr's method may be used.

It is important to realise the limitations imposed by assumption 3 (above). If all individuals are not equally catchable vast errors can occur (see Bishop and Bradley 1973). Any data for analysis must be taken from a population that is as homogeneous as possible. This may demand separate analyses of sub-populations (e.g. The sexes may have to be treated independently.) Any one sub-group may show variability (e.g. polymorphism) that will influence the probability of capture or recapture, so further divisions may be needed. Zoological insight used to assemble data from organisms into homogeneous groups will improve estimates of all parameters obtained from the population models listed in Table 1. If the nature and limitations of a method are understood then it is frequently convenient to use a computer to analyse data. Sources of suitable computer programs are tabulated.

EXAMPLES AND DISCUSSION

Dowdeswell, Fisher and Ford (1940) provide data from a population of the blue butterfly *Polyommatus icarus* on Tean, Isles of Scilly, U.K. These have been presented in such a way that they can be re-analysed to show the sort of estimates that can be obtained from Fisher and Ford's (1947) model (Table 2).

The units in the Fisher and Ford data trellis (Table 2) are marks not animals (it is a Type A trellis in the sense of Leslie and Chitty (1951)). A butterfly caught on 26th August and recaptured on 29th and 30th August contribues one "mark" to 29th August and two "marks" to 30th August. This model also

Table 1

Summary of properties of some popular capture-recapture models. It is essential that animals involved in multiple-recapture studies should be given a date specific mark at every capture or (preferably) an individual mark.

MODEL	No. of samples required	Rate of loss	Rate of gain	Parameters estimated	Best worked example	Computer program	Remarks
Lincoln Index	2	0 Constant 0	0 0 Constant	$P_1 = P_2$ P_1 P_2	-	-	To be used when only two samples are available.
Fisher and Ford (1947)	3 or more	Constant	Variable	(a) P for every sample time except first. (b) single constant survival rate (see remarks). (c) gains and losses.	Re-analysis of data of Dowdeswell, Fisher and Ford (1940) by R. J. White. Available on request from J. A. Bishop.	White and Sheppard in Bishop and Sheppard (1973)	Model calculates a single survival rate which is assumed to remain constant for duration of experiment. Requires less data (recaptures) than Jolly's and Manly & Parr's models (Bishop & Sheppard 1973).
Jolly (1965)	3 or more	Variable	Variable	(a) P for every sample time except first and last. (b) survival rate for each inter-sample period except last two. (c) gains and losses.	Jolly (1965) and Southwood (1966)	Davies (1971)	Calculates separate survival rates for inter-sampling periods. These assume that every animal has the same chance of surviving until next sample (i.e. mortality is independent of animals age).
Manly and Parr (1968)	3 or more	Variable	Variable	as by Jolly's model	Manly and Parr (1968)	Calculations simple but program by J. S. Bradley & R. J. White available from J. A. Bishop.	Calculates a separate survival rate for inter-sampling periods. These do not assume that mortality is independent of age.

Table 2

Fisher and Ford type data trellis and estimates of parameters for a population of the blue butterfly Polyommatus icarus on Tean, Isles of Scilly, U.K., 1938. (Data from Dowdeswell, Fisher and Ford 1940) Bailey's correction has been used in the calculation of population estimates.

			Date of marking								
	Captures	Releases	Aug. 26	27	29	30	31	Sep. 2	3	6	7
26 Aug. 1938	40	40									
27	43	40	5								
29	13	12	0	3							
30	52	50	3	8	5						
31	56	51	6	12	6	15					
2 Sept.	52	52	4	10	3	16	14				
3	50	50	4	5	1	11	5	14			
6	15	15	1	1	1	3	1	5	5		
7	20	20	1	1	2	3	2	7	8	6	
8	7	0	0	0	0	2	2	4	1	0	4

N.B. The population was not sampled on 28th Aug., 1st, 4th, 5th Sept.

TOTAL DAYS SURVIVED BY MARKS = 788

DAILY SURVIVAL RATE = 0.82831

DATE	MARKS IN POPULATION		POPULATION SIZE		GAINS+	LOSSES+
	NO.	%	RAW	SMOOTH*		
27 Aug	33	13.6	243	204		
28	61			193	25	35
29	50	28.6	176	170	10	33
30	52	32.1	161	148	7	29
31	84	70.2	120	123	1	25
1 Sept	112			108	5	21
2	93	90.6	102	114	25	18
3	120	80.4	149	120	25	20
4	141			112	12	21
5	117			94	2	19
6	97	112.5	86	76	2	16
7	92	147.6	63	65	1	13
8	93	175.0	53	57	4	11

TOTAL GAINS = 116

TOTAL LOSSES = 262

* Third order harmonic running means. + Calculated using smoothed population estimates.

Table 3

Basic capture-recapture data collected from a population of the burnet moth Zygaena filipendulae at Dale, Pembrokeshire, U.K. The complete history of each recaptured individual is shown (capture or recapture indicated by 1) (from Manly & Parr 1968).

JULY 1968				
19	20	21	22	24
1	1	1	1	1
1	1	1	1	
1	1	1		
1	1	1		
1	1	1		
1	1	1		
1	1	1		
1	1	1		
1	1	1		
1	1	1		
1	1			1
1	1			1
1	1			1
1	1			1
1	1			
1	1			
1	1			
1	1			
1	1			
1	1			
1	1			
1	1			
1	1			
1	1			
1		1	1	1
1		1	1	1
1		1	1	1
1		1	1	1
1		1	1	1
1		1	1	1
1		1	1	1
1		1		
1			1	1

	JULY 1968				
	19	20	21	22	24
	1			1	1
	1				1
		1	1	1	
		1	1		1
		1	1		1
		1	1		1
		1	1		1
		1	1		
		1	1		
		1	1		
		1	1		
		1		1	1
		1		1	
		1		1	
		1			1
		1			1
			1	1	1
			1	1	
			1	1	
			1	1	
			1	1	
			1		1
			1		1
			1		1
			1		1
			1		1
			1		1
			1		1
			1		1
				1	1
				1	1
				1	1
				1	1
				1	1
Number captured once only (on day indicated) and not included above.	21	12	13	9	19

Table 4

Type A and Type B data trellises derived from data in Table 3.

Type A data trellis (for Fisher and Ford's model). Units under 'Date of Marking' refer to marks not animals.

Date	Captured	Released	Date of marking 19	20	21	22
19	57	57				
20	52	52	25			
21	52	52	19	20		
22	31	31	9	6	12	
24	54	54	15	12	20	15

Type B data trellis (for Jolly's model). Units record date of last capture of an animal recaptured.

Date	Captured	Released	Date of marking 19	20	21	22
19	57	57				
20	52	52	25			
21	52	52	8	20		
22	31	31	2	3	12	
24	54	54	1	6	13	15

Table 5

Estimates of population size and daily survival rate obtained from data of Table 3 by Fisher and Ford's, Jolly's and Manly and Parr's models. (Bailey's correction has not been used)

Date	FISHER & FORD	JOLLY		MANLY AND PARR	
July 1968	Population Size	Pop.Size	Survival rate	Pop. Size	Survival rate
19	-	-	0.78	-	0.76
20	91	93	0.74	90	0.71
21	102	98	0.76	97	0.69
22	116	106	-	93	-
23	-	-	-	-	-
24	75	-		-	

Fisher & Ford survival = 0.801

The expectation of life is approximately $4\frac{1}{2}$ days. This can be estimated by $\frac{1}{1\text{-survival rate}}$ if all deaths occur just before sampling or by $\frac{-1}{\log_e(\text{survival rate})}$ if deaths are at random throughout the intersampling period.

requires a quantity called the total days survived by all marks. On the 29th the mark of the 26th has survived 3 days and on the 30th 4 days. In addition the new mark of the 29th has survived one day. Therefore this animal contributes 3 + 4 + 1 days to the total. The units in the Jolly data trellis refer to individual animals and the date they were last captured (i.e. it is a Type B trellis). Examples of Types A and B are given in Table 4. The Fisher and Ford method uses the information in the data trellis to calculate a 'survival' rate per unit time for marked animals. This can then be used to allow for loss of marks (by death or emigration) in a modified Lincoln Index calculation. Estimates of population size then can be obtained and gains (birth and immigration) calculated. The complete analysis is given in Table 2. A worked example of Dowdeswell, Fisher and

Ford's data by Mr. R. J. White, Department of Zoology, University of Liverpool, is available from J. A. Bishop. The calculations for Jolly's method are given by Jolly (1965) and Southwood (1966).

Manly and Parr (1968) present a set of results from a capture-recapture investigation of the burnet moth *Zygaena filipendulae*. They also provide a worked example of their model based on this data. Their data are tabulated in a manner that allows re-analysis by Fisher and Ford's and by Jolly's methods. The original data and the Type A and Type B trellises appear in Tables 3 & 4. The estimates of the population parameters provided by all three models are also given (Table 5).

We believe that these examples emphasize the advantages of modern capture-recapture methods. They also indicate the desirability of presenting, where possible, the original data in a simplified but coherent form (Table 3).

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